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THE SELECTION OF FOOD-PLANTS BY INSECTS, WITH SPECIAL REFERENCE TO LEPIDOPTEROUS LARVÆ[1]

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The instinctive behavior exhibited by phytophagous insects in the selection of their food-plants is always a matter of interest to entomologists, and it is one of the fundamental principles underlying the application of entomology to agriculture, horticulture and forestry. Nearly all insects show a great fixity of instinct in this respect, but a most cursory examination of the habits of almost any group will reveal a considerable variation among different species, particularly with reference to the number of plants regularly utilized as food and in the selection of closely related or of very diverse plants.

The origin and development of the association between insect species and plant host has been the basis for a considerable amount of speculation which has increased in proportion to the additional knowledge continually added through field observation, collection, and rearing of insects.

Before considering any of the theories advanced to account for the association of insects with definite plants, I shall attempt to give a very brief account of the salient facts concerning food-plants which appear to be sufficiently definite for orderly arrangement, restricting the discussion for the present, mainly to one of the better known orders of insects.

The term phytophagous with reference to insects is commonly employed in a considerably restricted and rather inaccurate sense, including only those species that feed upon the higher plants, meaning by these the ferns and flowering plants. Only an extremely small, almost negligible, proportion subsist upon ferns, so that from a practical standpoint, we would include only those feeding upon the Spermatophytes. This usage has developed on account of the fact that the fungi which have many insects feeding upon them, do not ordinarily engage the attention of the economic entomologist, and for convenience it is acceptable in the present connection, as very little is known concerning the specific hosts of insects living in fungi. Furthermore, the food-plant is ordinarily understood to mean the species upon which the larval or growing stages occur, for although it is common to find both the young and adult insects of the same species subsisting upon the same plant, it occurs also very frequently that the food of the larvæ and imagines of holometabolous insects is of entirely different nature. Among the many other truly phytophagous insects living in fungi are a number of families of beetles, for example, which develop in the tissues of the larger, fleshy fungi and many of these mycetophagous insects undoubtedly show a very close association with certain species of fungi. In addition, some insects subsist upon the lower fungi, yeasts and even bacteria. The biology of these latter is very imperfectly known in nearly all cases, owing to the greater difficulties attendant upon studies dealing with them. The well-known fungous-growing ants and termites and the ambrosia beetles actually cultivate certain fungi for food and other insects (undoubtedly a far larger number than is now known) subsist upon various microorganisms, although they are, to the eyes of the casual observer, feeding directly upon the substrata which really nourish the microscopic fungi, yeasts or bacteria, that in turn form the actual food for the insects. As already said, however, these symbiotic relations are in most cases only very poorly understood, and they are entirely outside the scope of the present discussion.

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[1] Contributions from the Entomological Laboratory of the Bussey Institution, Harvard University, No. 168.

As distinguished from those of predatory, parasitic and saprophagous habits, the phytophagous insects represent probably nearly half of the known species, and a considerable proportion of the several orders of insects contain at least some species that are phytophagous in the sense indicated above. Some of these, like the Orthoptera, are very primitive, while others of probably equal or even greater antiquity are not phytophagous, so that it is difficult to say whether the earliest true insects were vegetarian, predatory or saprophagous.[2] This question is perhaps not a very important one, for, as will be pointed out later, a change from one type of food habits to another has actually taken place independently in several families of the highly specialized Lepidoptera.

As we might naturally expect, it is possible to point out in a very general way a progressive specialization in the selection of food-plants which parallels to some degree what appears to have been the path of evolution among insects, as determined from the criteria furnished by comparative anatomy, development and paleontology. Thus, the primitive Orthoptera appear to select their food-plants with but little discrimination, while the Lepidoptera and phytophagous Hymenoptera exhibit almost unerring accuracy in their instincts to choose certain plants and consistently to ignore all others. Beyond this, however, it is not easy to make any broad statements, for among the most highly specialized groups we find a great variability, at least in the number of food-plants admitted to the menu, as well as in regard to the botanical relationships of the plants regularly selected.

It may be argued that selection of food-plants is a somewhat dubious expression and that it may not accurately represent the condition of affairs from the standpoint of the larval insect. In most cases the larval food-plant is really chosen by the adult female, who places her eggs upon certain plants which then become of necessity the food of the resulting larvæ, which could not very readily migrate to another kind of plant even should they be willing to do so. This objection is readily met by experimental evidence, for every entomologist is fully aware of the fact that it is ordinarily quite impossible to rear insects of restricted food habits upon other than their normal food-plants. It is true that an acceptable plant may sometimes be found by those familiar with the vagaries of related species of insects, but in such cases we may safely assume that the experimentally selected plant may later prove, in at least some cases, to be one sometimes picked out for food in nature.[3] It would be an unwarranted assumption, therefore, to suppose that the maternal instinct of oviposition does not at the present time represent fairly well the tastes of the larva. We may reasonably ask, however, whether the selection of the mother may not have impressed itself upon the larva after continual repetition or whether the taste acquired by the continual feeding of the larva may not persist into the adult, just as fondness for sweets may become a lifelong attribute in examples of the human species pampered in youth by indulgent mothers. During the progress of evolution as food-habits have become fixed, it is evident that any changing tastes on the part of the larva must have become a part of the egg-laying instincts of the mother, through the action of natural selection or otherwise, before any change of food-plants could occur. On the other hand, any change in the instincts of oviposition, not incompatible with larval tastes, might quickly become a definite characteristic of the species. If any adults should select unsuitable plants their progeny would quickly perish. The maintenance of definite preferences can thus be seen to be readily perpetuated through the action of natural selection in the survival of the fittest strains and the elimination of the unfit ones. It will be evident later, however, that subsistence on many food-plants would appear to have originated after the manner of mutations, and it will, I think, be evident that we should attribute these, at least in part, to chance mutations or aberrations of instinct in the parent insects.

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[2] This last term is rather ambiguous and is rapidly becoming still more so in the light of studies recently made upon insects that subsist upon microorganisms.

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[3] It may also be noted that those experienced in rearing caterpillars are frequently able to rear species of unknown habits on certain plants (*e. g.*, chick-weed, *Cerastium*) on which they do not normally feed, but which are acceptable to many larvæ in the absence of their natural food-plant.

Before dealing specifically with the selection of food-plants, it is necessary to classify in a general way the types of food-habits generally met with in insects. Thus, Reuter applies the terms Pantophaga to omnivorous insects, Phytophaga and Sarcophaga to vegetarian and carnivorous ones respectively and Necrophaga and Coprophaga to those living upon dead animals and excrementitious material. Among the Phytophagous forms he would further distinguish monophagous and polyphagous species on the basis of the number of food-plants which they utilize. Although satisfactory so far as it goes, this fails to include several categories commonly referred to by entomologists and for the present purpose it can be readily enlarged as follows:

Pantophaga

Phytophaga
Monophaga
Oligophaga
Polyphaga

Sacrophaga
Harpactophaga
Entomophaga

Saprophaga
(Partly subdivided as below)

{Microphaga, Mycetophaga}
{Necrophaga, Coprophaga}

In this arrangement a distinction is made between vegetarian species with a single food-plant (Monophagous), those with several definitely fixed ones (Oligophagous) and those with quite indiscriminate food-habits (Polyphagous). On the other hand predatory species (Harpactophagous) and entomophagous parasites are distinguished, as each form a very large and important group. Many necrophagous and coprophagous species really subsist on bacteria, fungi, etc., and these may perhaps be better designated as microphagous and mycetophagous.

Among phytophagous insects, the polyphagous habit is probably the most primitive and the monophagous one the most highly specialized. It is not rare, however, to find all three types represented in otherwise very homogeneous groups. The Lepidoptera, for example, form an enormous complex of species, practically all of them phytophagous, the majority feeding upon a very restricted series of plants and representing the oligophagous habit, with a smaller series of apparently monophagous forms and a few secondarily polyphagous ones. Fortunately also, the food habits of this order as a whole, are better known than those of other insects and it can be examined with less chance of error than perhaps any other group of equal extent.

As already stated, nearly all of the larvæ of the Lepidoptera are phytophagous at the present time and there can be no question that since the order has existed this condition has prevailed. Owing to a change in the form of the trophi during metamorphosis by which the adult Lepidoptera develop haustellate or sucking mouthparts, the food of the imagines is entirely different from that of the larvæ and they subsist upon liquids, mainly the nectar of flowers.

We may then classify the food-habits of the larvæ roughly as follows:

Food Material	Frequency of Utilization
Plant-food	Nearly all of the species
Bacteria	Probably none
Fungi	Almost none
Lichens	A very few, mainly in one family
Mosses	Almost none
Ferns	A very few
Flowering plants	Probably about 99 per cent.
On foliage	A large majority
In flowers	A few
In aquatic plants	A very few
In roots	A few
In tissue of herbaceous plants	A rather small number
In wood of shrubs and trees	A rather small number
In dried seeds, fruits, etc.	A very small number mainly in one group
Animal food	
On other living insects	A few isolated cases
On material of animal origin; wool, horn, beeswax, etc.	A very few, mainly in one group

From this it will be seen that while the food-habits are very homogeneous, isolated cases occur where certain species have departed very strikingly from their more conservative relatives. Among these, the most interesting are those which have become carnivorous. Thus, we have in the eastern United States, a small butterfly, *Feniseca tarquinius,* which feeds upon plant lice occurring on alder. In our southwestern states there occurs also a moth of the genus *Epipyrops,* typical of the family Epipyropidæ, utterly unrelated to *Feniseca,* which feeds upon Homopterous insects of the family Fulgoridæ, and other species of *Epipyrops* are known to have quite similar habits in the orient. Also *Thalpochares,* a moth of the family Noctuidæ, is known to feed upon aphids and scale insects in Europe and Australia. Similarly the caterpillars of the Australian Cyclotorna is ectoparasitic on Homoptera of the family Jassidæ, and the larvæ of *Zaphiodiopsis* feed upon other caterpillars. A still further and more extraordinary modification is in the larva of the British butterfly, *Lycœna arion,* which is herbivorous in its early stages, but enters the nests of ants to prey upon the ant-larvæ during its final period of growth. Other scattered cases of predatory caterpillars are known, including other butterflies and moths of several families. With these the most striking feature is that the prey almost always consists of Coccids or Aphids. This association is probably due to the fact that these Homoptera are sessile or slowly moving creatures, commonly present where caterpillars occur and therefore apt to attract those of carnivorous instincts. Of interest in cennection with this, is the fact that certain phytophagous caterpillars may become temporarily carnivorous, quite regularly or under the stress of circumstances. Thus, the very abundant and destructive corn ear-worm, *Heliothis obsoleta,* commonly lays a number of eggs on the silks of a corn-ear, although nearly aways only one caterpillar finally survives in the interior of the ear where it does most of its feeding. Here the elimination is due to a cannibalistic instinct of the caterpillar which results in the disappearance of the excess individuals, notwithstanding the fact that there is food enough for a considerable series in a single corn ear. A similar cannibalistic habit has been reported in *Hadena* and *Agrotis,* two other genera of the same family, and no less than 75 species of European Lepidopterous caterpillars are known to be occasionally predatory through temporary aberrations of their trophic instincts.

With such plasticity of behavior in several diverse families and even with *Lycæna arion* and certain small moths exhibiting a change in food habits during ontogeny, it is not difficult to regard the origin of sarcophagy in Lepidoptera as due to independent changes which have become firmly fixed in individual species or genera.

The habit of certain Tineid moths, including the clothes-moth (*Tinea*) and some of its relatives, to feed upon wool and other materials of animal origin is well known, and other non-domesticated forms of the same group exhibit similar food-habits. One African species of *Tinea* lives at the base of the horns of a large water antelope, where it forms tubes similar to those constructed by some other Microlepidoptera. The bee-moth, *Galleria mellonella,* a commensal in the hives of the honey-bee, subsists upon beeswax and bits of refuse said to contain about 20 per cent. of nitrogenous matter. Practically all of the caterpillars that subsist on foods of animal origin are more or less closely related, but not sufficiently so for us to entertain for a moment the belief that the habit has not originated independently in numerous instances. Why it should be restricted to a few groups in one part of the order, may, I think, be explained on the following basis. Among the Microlepidoptera only do we find forms able to subsist upon plant materials containing a very small amount of water (*e.g.,* seeds, dry fruits, grain, flour, etc.) as distinguished from the tissues of growing plants. Even in the wood of trees, tunneling larvæ remain in a moist burrow where evaporation is very slow. Similarly the animal materials utilized as food are very low in water content. That we do not find Lepidopterous larvæ in moist material of animal origin is no doubt due to the fact that they do not appear to be adapted for subsistence upon the abundant microorganisms present in such materials.

Passing to a consideration of the phytophagous Lepidoptera, by far the greater part of the order remains to be dealt with. As indicated in the tabulation, practically all of these occur on the higher plants and feed almost always upon living tissue. The latter is true almost without exception of the leaf-feeding forms, although one of our common moths of the eastern states, *Pyromorpha,* is known to live upon dead and decaying fallen leaves and another of our small moths avails itself of hemlock chips. Among those which live in woody tissue, some prefer weakened or sickly trees or unhealthy branches, but almost none occur in dead wood.

Of those living on the lower plants, one small family of moths, the Lithosiidæ, subsist upon lichens and they are almost the only ones affecting these plants. This family is far from primitive, so that its association with a series of lower plants could have no significance, even if it were definitely known that the lichens are a very old group, which does not seem probable.

Mycetophagous forms of Lepidopterous caterpillars are of very unusual occurrence, in spite of the fact that several large series of beetle larvæ develop in fungi. They are found, however, and there are in North America at least two species of *Tinea* which have been bred from these plants.

In spite of the similarity of their foliage to that of the flowering plants, ferns do not commonly serve as food plants for insects. They are, in fact, strikingly immune from insect pests of all sorts. This is hardly what might be expected from the long presence of this group of plants, their enormous development in the past, and their persistence at the present time in quite considerable abundance. Why they should be so sparingly selected as food plants does not seem to have been adequately explained.

The use of Phanerogams as food-plants is so general that it is possible to gain a much clearer insight into the conditions pertaining to them than is the case with other plants. In general the food habits of butterfly larvæ are more fully known than those of the moths, on account of the smaller number of species and the general interest taken by amateurs in this group.

An account, very complete at the time, has been given by Scudder of the food-plants of the butterflies of eastern North America.[4] A tabulation of the food-plants included in this list shows several interesting features. Fifty-five families of plants are included (not taking into account several larvæ feeding on conifers and our one predatory species) and the list contains a very representative series, drawn from both the Monocotyledons and Dicotyledons in approximate proportion to the number of species of these two sections. It is noticeable, however, that several common families, the Iridaceæ, Orchidaceæ, Caryophyllaceæ, Euphorbiaceæ, Vitaceæ, Primulaceæ and Rubiaceæ are entirely omitted, that only one species occurs in the Labiatæ, or on the Umbelliferæ, and that only a very few affect Compositæ. We may readily see that the generally strong-scented Labiatæ and Umbelliferæ and the milky Euphorbiaceæ might require great adaptation on the part of larvæ eating them,[5] but the omission of the other families if not entirely a matter of chance must rest upon some less evident basis than the foregoing. Among the other plant families the number of species of caterpillars compared to the number of eastern American genera, included in each family that is fed upon, varies exceedingly, from 1:100 to 1:1 or even 1.6:1 in the case of the Rutaceæ. The average is about 1:4, but there is no tendency for the ratios to fall near the mean and their distribution if not a matter of chance, must have been determined in relation to their environment, no doubt to a great extent by their struggle for existence with other plant-eating forms.

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[4] This list has been used as a whole as it is complete in itself, and to attempt to add to it and emend it by the present writer, from more recent literature, would improve it but little for the present purpose.

[5] This is true only of the butterflies in this list; many other leaf-eating larvæ feed in abundance on these plants.

If we examine the food-plants of the genera or higher groups of butterflies, we find that most of them exhibit well-marked preference for certain, usually related plants. The food-plants of the British butterflies are unusually well known, and Tutt has recently given in his work on "British Butterflies" a digest of their preferences which he finds to be closely similar to those of the nearctic forms previously considered by Scudder. Gathering his more definite data together and using his terminology for the groups, the food-habits may be tabulated as follows:

Vanessids	Urticaceæ Compositæ, etc.
Argynnids	Violaceæ exclusively
Brenthids	Violaceæ generally
Melitæids	Various plants
Pierids	Cruciferæ essentially
Anthocarids	Cruciferæ essentially
Limenitids	Various plants
Apaturids	Various plants
Satyrids	Gramineæ almost entirely
Coliads	Leguminosæ almost entirely
Gonepterygids	Rhamnaceæ
Ruralids	Various plants (more or less fixed in some subdivisions)
Lycænids	Diverse food-habits
Chrysophanids	Polygonaceæ almost exclusively
Urbicolids	Various plants
Sub-groups Thymelicines	Gramineæ mainly
Urbicolines	Gramineæ mainly
Cyclopidines	Gramineæ mainly
Hesperiines	Leguminosæ and various other plants
Papilionids	Various plants; several groups with particular food-plants

Viewed in this way, it is seen that barring many exceptions, there is a general tendency, much more pronounced in some groups than in others, to select plants of very specific families or even genera. This must not be understood to mean that the individual species of insects affect indiscriminately many or all members of the plant group, but that their normal food-plant or plants do not fall outside the group. With the exceptions in mind, the fixity of the instinct to feed on only certain kinds of plants is all the more extraordinary, for we cannot readily dismiss it as a physiological or nutritional necessity.

An interesting light upon the effect of the environment in influencing the selection of food-plants, is furnished by several widely distributed species and genera of butterflies. Thus several species of *Vanessa* have quite identical food-habits throughout the entire holarctic region and the same is true of several very closely allied palæarctic and nearctic species belonging to the same group, while, as mentioned above, the general food habits of the larger groups run closely parallel among their representatives on the two continents. Still more interesting in this respect are the butterflies of the closely related genera *Catopsilia* and *Callidryas* which restrict themselves to the Leguminous genus *Cassia*. These butterflies occur in the nearctic, neotropical, Indo-Malayan and Australian regions and such species as have been reared show this preference, which is probably universal. The well-known genus *Papilio* supplies some similar peculiarities in that several world-wide groups of the genus are restricted to certain closely related groups of plants (*e. g.*, *Aristolochia, Citrus,* etc.). On the other hand, one North American species, the common *Papilio glaucus,* is known to affect food-plants belonging to no less than fifteen different families of plants. With such constancy in the most remote quarters of the globe among related species of this genus and with one species in a single region regularly developing on the most diversal plants, we must believe that the fixed instincts of some species are not to be led astray by the many temptations offered even by the varied plants of widely separated zoological regions, while those of other species are so loose that they restrict their owners only to a comparatively very small extent. Such conditions certainly point to instinct as the determining cause of food selection, rather than physiological adaptation to specific kinds of plants.

In connection with cosmopolitan butterflies, Scudder noted many years ago, that there are no species of remarkable distribution known to feed upon Leguminosæ or grasses, although these plants are cosmopolitan and harbor many species. I am inclined to believe, however, that this has no significance, particularly in view of the aforementioned Coliads that feed upon *Cassia* in various parts of the world.

Many other groups of Lepidoptera conform quite closely in food-habits to the butterflies, although some show greater diversity, especially in affecting different parts of the plant, and it may be said in general that the larger moths are less apt to be monophagous than the butterflies.

Among the hawk-moths or sphinx-caterpillars several subfamilies show a restriction to groups of related plants, while others do not. Thus in this cosmopolitan family, one subfamily (Chærocampinæ) feeds on Vitaceæ, with an admixture of diverse other plants, another (Macroglossinæ) on Caprifoliaceæ exclusively, another (Sphingineæ) to a great extent on Oleaceæ together with other plants as different as Conifers, Solanaceæ, Euphorbiaceæ and Labiatæ, while one (Smerinthinæ) exhibits no apparent preference.

The family, Aegeriidæ, or clear-winged moths, live in the larval stage in the interior of plants, tunneling through the tissue. They affect a very wide series of plants, herbs, shrubs and trees, as can be seen from the following abbreviated list which represents the range in habits of some of our eastern North American representatives; stems of Cucurbits, *Vernonia,* blackberries, currant, grape; wood of pine, willow, lilac, maple, oak, peach; roots of *Clematis,* persimmon, blackberry, *Eupa-*

torium; stumps of oaks cut the previous year; and oak-galls. Notwithstanding such diversity within the family, the individual species are nearly monophagous, or oligophagous on related plants. Such a condition would seem to have arisen through sudden mutations in instinct rather than from numerous smaller variations having a selective value, for in the latter case we should find polyphagous forms developing in some places at least.

Another, much smaller family of rather generalized structure, the wood-boring Cossidæ, have habits similar to many of the Sesiidæ, but their selection of food-plants is very different. Typically they are oligophagous, but some species, including the well-known and destructive shade-tree pest known as the leopard-moth (*Zeuzera pyrina*) introduced from Europe into the eastern United States, has been bred in this country from an almost endless variety of shrubs and trees, as it has been in Europe also. As listed by Chapman, the American food-plants belong to twenty-two families of plants and to nearly fifty genera. Almost all that can be said of the leopard-moth's bill-of-fare is that it includes no conifers.

Cossus ligniperda, another European species is strongly polyphagous, but many of the exotic species appear to avail themselves of a rather restricted diet. As this latter is perhaps due to lack of knowledge, it may be unwise to draw any conclusions at present.

In other families of moths the same phenomenon is frequently encountered. The large group of Noctuidæ, comprising the owlet-moths, feed mainly upon the foliage of a wide rang of plants, while the list of food-plants for the numerous species varies greatly in extent. To attempt to classify the food-habits of this group would require much time and space, but it may be said that there are species in certain genera, as, for example, the cotton boll-worm, which appear to have rather suddenly enlarged their range of food-plants as compared with that of related species of the same genera.

In regard to the uniformity of food-plants during ontogeny, the statement has been made that some Lepidopterous caterpillars occur on a greater range of plants when young, or at least that they will readily feed upon certain kinds during the earlier instars, and refuse them later, so that their diet becomes more restricted as growth progresses. This statement has been in turn used as an argument that oligophagous forms are derived from more restricted feeders, and that they repeat in a way their history by the limitation of their food-plants during successive instars.

Some elaborate experiments on the feeding habits of the gipsy-moth reported on by Mosher tend to discredit this supposition, however. As is well known, the gipsy-moth occurs on a wide range of plants, but shows well-marked preferences for certain among them which represent its favored food. These experiments were carried out in the extensive detail possible only when dealing with insects of great economic importance, and although planned for another purpose, furnish valuable data upon this point. It appears that on a number of their numerous food-plants, the gipsy-moth caterpillars show an inability or at least an unwillingness to feed either during the very early or during the later larval stages. On some kinds of trees the early larvæ failed to develop and on others the latter stages did not feed, although the young ones did so. This diversity of behavior is in part due to the fact that young larvæ cannot usually feed upon conifers, while the older ones eat the foliage of these trees voraciously; but it is by no means due to this alone, so that we can say that the juvenile preferences of the larvæ become transformed or changed as growth progressed. With an active polyphagous caterpillar like the gipsy-moth in which the larvæ often migrate to other species of plants during growth, it is possible for such changes in diet to take place regularly in nature, although such could not ordinarily occur with oligophagous species without tending greatly to reduce the chances of the species to survive. As the necessity for migration is most acute in the case of very abundant species, they are open to more temptations to avail themselves of a variety of foods and we find that it is usually the most abundant species of any group that are polyphagous. Conversely we may say also that polyphagy, when present, greatly increases the chances for the larvæ to secure the necessary amount of food for complete growth and tends to cause the species to become excessively abundant. Once under headway, these two processes will act together and result in the production of dominant species that tower above their fellows. Examples of this are seen in the gipsy-moth,[6] the *Cecropia*-moth, the army-worm, *Papilio glaucus* mentioned above, the woolly bear (*Isia isabella*), etc. We must not lose sight of the fact, however, that this is only one of many factors influencing dominance. The milkweed-butterfly, one of our most abundant native species develops on a very common plant (*Asclepias* almost exclusively) and is thought also to be a protected species.[7] Its dominance may be interpreted, like that of many destructive agricultural pests, as due to a plentiful and unfailing food supply, coupled with other pre-requisites inherent in the insect itself.

In spite of the many exceptions and variations which have been enumerated, the fact stands out clearly that the Lepidopterous insects show a very fixed instinct to select definite plants for larval food; that many are extremely precise in this respect, some less so, and others quite catholic in their tastes. Furthermore there is much to show the existence of a so-called "botanical instinct" in species, genera and even families, whereby evidently related plants and these only serve as food. A few species have departed from the general habit so far that they have become carnivorous, and among the others we find every gradation between the extremes of monophagy and polyphagy.

It has been claimed that the food habits may be modified experimentally, in that caterpillars reared on a strange plant (where they could be induced to select it) give rise to moths whose progeny more readily accept the new plant. It is very difficult to accept such evidence, at least as having any general application, without very clear and incontrovertible proof. If such transformations can occur so easily and become hereditary so quickly they should have entirely destroyed the coherent habits now existent, during the enormous period which has elapsed, for example, since the violent-feeding Argynnids were differentiated, since the holarctic and nearctic Vanessids have been separated, or while the worldwide Aristolochia-feeding Papilios were attaining their present distribution. That such a change has actually occurred in the case of other groups seems equally evident, although, as has been shown, we can more easily believe that they may have arisen through mutations in maternal instinct not incompatible with larval tastes and then only in extremely rare cases and confined to certain groups.

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[6] This is true also in the native habitat of this species, aside from the decimation by parasites which occurs more abundantly in Europe.

[7] *i. e.*, distasteful to its enemies and exhibiting warning coloration.

With a knowledge of the specificity of proteins in different living organisms and their apparent differentiation as a replica of the genealogical history of the animal and plant kingdoms, has come the suggestion that the dependence of monophagous or oligophagous insects upon specific plants rests upon a physiological basis, and that particular proteins or vitamines are an actual necessity for growth and development. A survey of the field does not seem to bear out this supposition, however plausible it may appear at first sight. With monophagous larvæ, it will serve as a reasonable explanation, and with oligophagous ones also so far as the individual species are concerned, especially where such species select a series of related plants. With those that select only a few plants, however, and at the same time such as are evidently not closely related, it does not seem so appropriate. It is when we compare the lists of food-plants of several oligophagous species that it appears to fail completely to meet the requirements. Thus we find, referring again to our North American butterflies, such combinations as Leguminosæ with Pinaceæ, or with Rhamnaceæ, Polygonaceæ, Cupuliferæ in the case of different larvæ. More uniformity should certainly be expected if the selection of diverse plants depended upon the actual chemical characteristics of the plant tissue. We should have also to assume that the digestive functions of the cecropia caterpillar with its sixty-odd food-plants were fundamentally different from those of monophagous caterpillars.

There is much in the behavior of certain species to suggest that food-plants are selected on the basis of odor by the parent female and also accepted on the same basis by the larvæ. Experiments with cabbage butterflies by Verschaffelt and others show that these insects are attracted by the mustard oils present in these plants, and it has also been shown that caterpillars will feed on other plants which have been treated with one of these oils. Similar behavior in the most diverse insects is also known in the attraction exercised by specific fermentation products (*e.g.*, to *Stomoxys, Drosphila,* etc.). The distaste of mosquitoes for oil of *Citronella* is well known, as is also the attractiveness of this same substance for fruit-flies of the genus *Dacus.* That the same cabbage butterflies have definite dislikes in the way of plant odors has recently been claimed by the Russian entomologist Schreiber, who found that *Pieris brassicæ* would not attack cabbages planted in close proximity to tomatoes. *Pieris rapæ* does not seem to behave similarly, however, and this dislike is probably not general among the crucifer-eating Pierids.

Very recently McIndoo has published some observations showing that caterpillars readily react to the odors of several essential oils and to those of various plants. This, taken together with the fact that *Pieris* will feed upon strange plants treated with mustard oil, would suggest that odor is an important factor in the selection of food-plants. Queerly enough, however, he found that the response to their own food-plants was no more rapid than to the other substances, and even slower in some cases. As the smearing of the oils of one plant on another does not occur in nature, the important point to discover is whether there is really any similarity of odor in the several plants of diverse groups that are sometimes utilized by a single species of insect. The facts alluded to above in regard to the wide variety of selections made by different species would seem to answer this question in the negative, as would our own human sense of odor, which latter may, of course, not be reliable when dealing with a group of animals so different from man. We may, I think, rest assured that odor frequently guides the insects to their food-plant, but we can not believe that oligophagous or polyphagous species have become accustomed to a variety of plants due to a confusion of similar odors. There does seem, however, to be one very striking exception to this among the Pierid butterflies. As said before, these butterflies are confined to Cruciferæ almost exclusively, but one of our species not infrequently occurs on the garden ''nasturtium'' (*Tropæolum*). That the pungent taste of this plant is much like that of a Crucifer is well known and further attested by the common name, as the true nasturtium of the botanists is a genus of Cruciferæ, while the garden nasturtium is a Geraniaceous plant.

On account of the very close biological association between insects and plants in many ways it is true that the two have been mutally specialized until they have become highly modified in reference to one another, but this is not the case with food-plants, as no benefit ordinarily accrues to the plants and any idea of parallel evolution must be restricted to a development of undesirable attributes on the part of the plants and adaptations on the part of the insects to overcome such barriers to feeding.

To avoid these numerous difficulties, it seems clear that the selection of food-plants by the Lepidopterous insects so far mentioned, must be considered as dependent upon one or several of a number of factors. Among these we must include the following:

1. The odor of the plant, and also its taste, which is no doubt closely connected with odor. Associations reasonably placed in this category would be the oligophagous species occurring, for example, on various Cruciferæ, various Umbelliferæ, and various Compositæ. An additional argument for the importance of this factor is seen in the less common utilization by the same insect of several plants in a family like the Solanaceæ[1] where a more or less similar odor does not become a family characteristic.

2. Some attribute of the plant, perhaps an odor but far less pronounced to our own senses than those mentioned above. Species restricted to plants like Leguminosæ or Violaceæ may be considered in this category. Undoubtedly there is some attribute of such plants which insects can recognize in a general way and not as a specific characteristic of some single plant species or genus. The "botanical instinct" of some caterpillars that has frequently been commented upon would appear to be an exaggerated power of recognition of this sort.

3. A similarity in the immediate environment or general form of the food-plant. The effect of something of this sort is seen particularly in oligophagous and also polyphagous caterpillars feeding mainly on trees or shrubs, such as the gipsy-moth, *Cecropia* moth, etc., and those of certain species like some of the Arctiid moths that feed upon a great variety of low plants.

4. Apparently chance associations that have become fixed, whereby diverse plants are utilized by oligophagous species. Secondarily polyphagous species show these in an exaggerated form. On account of their comparatively rare occurrence these seem to be analogous to structural mutations, although they appear to be strictly modifications of instinct. As has been pointed out on a previous page, these are much more apt to occur in some groups (families and genera) than in others.

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[8] Possibly in this family, however, the matter may rest upon a physiological basis, on account of the common occurrence of powerful alkaloids in these plants.